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## OCEAN RANCHING

**A. G. V. Salvanes**, University of Bergen, Bergen, Norway

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### Introduction

Ocean ranching is most often referred to as stock enhancement. It involves mass releases of juveniles which feed and grow on natural prey in the marine environment and which subsequently become recaptured and add biomass to the fishery. Releases of captive-bred individuals are common actions when critically low levels of fish species or populations occur either due to abrupt habitat changes, overfishing or recruitment failure from other causes. Captive-bred individuals are also introduced inside or outside their natural geographic range of the species to build up new fishing stocks.

At present 27 countries (excluding Japan) have been involved with ranching of over 65 marine or brackish-water species. Japan leads the world with approximately 80 species being ranched or researched for eventual stocking. This includes 20 shared with other nations and 60 additional species. **Table 1** shows an overview of the most important species worldwide. Many marine ranching projects are in the experimental or pilot stage. Around 60% of the release programs are experimental or pilot, 25% are strictly commercial, and 12% have commercial and recreational purposes. Only a few are dedicated solely to sport fish enhancement.

The success of ocean ranching relies on a knowledge of basic biology of the species that are captive bred, but also on how environmental factors and wild conspecifics and other species interact with the released. This article provides general information on life histories of the three major groups of animals that are being stocked, salmon, marine fish and invertebrates, and an overview of the status and success of ocean ranching programs. It also devotes a short section to the history of ocean ranching and

a larger section on how success of stock enhancement is measured.

### History

Ocean ranching has a long history going back to 1860–1880 that commenced with the anadromous salmonids in the Pacific. In order to restore populations that had been reduced or eliminated due to factors such as hydroelectric development or pollution, large enhancement programs were initiated on various Pacific salmon species mainly within the USA, Canada, USSR and Japan. In addition, transplantation of both Atlantic and Pacific salmonids to other parts of the world (e.g. Australia, New Zealand and Tasmania) with no native salmon populations was attempted.

Around 1900, ocean ranching was extended to coastal populations of marine fish. Because of large fluctuations in the landings of these, release programs of yolk-sac larvae of cod, haddock, pollack, plaice, and flounder were initiated in the USA, Great Britain, and Norway. It was intended that such releases should stabilize the recruitment to the populations and, thus, stabilize the catches in the coastal fisheries. There was, however, a scientific controversy of whether releases of yolk-sac larvae could have positive effects on the recruitment to these populations. In the USA the releases ceased by World War II without evaluation. In Norway evaluation was conducted in 1970 when it was shown to be impossible to separate the effect of releases of yolk-sac larvae from natural fluctuations in cod recruitment, a conclusion that led to termination of the program. Recent field estimates of the mortality of early life stages of cod suggest that only a handful of the 33 million larvae, an amount normally released, survive the three first months.

Larvae and juveniles of European lobster (*Homarus gammarus*) have been cultured and released along the coast of Norway for over 100 years. In 1889 newly hatched lobster eggs and newly settled juveniles were released in Southern Norway on an island which has its own continental

**Table 1** Main species which are captive bred and released in ocean ranching programs

English name	Scientific name	Country
<i>Salmonids</i>		
Atlantic salmon	<i>Salmo salar</i>	Norway, Iceland, UK
Pink salmon	<i>Oncorhynchus gorbuscha</i>	USA, Canada, Japan
Chinook	<i>O. tshawytscha</i>	USA, Canada
Chum salmon	<i>O. keta</i>	USA, Canada, Japan
Coho salmon	<i>O. kisutch</i>	USA, Canada, Japan
Sockeye salmon	<i>O. nerka</i>	USA, Canada, Japan
Masu salmon	<i>O. masou</i>	Japan
<i>Marine fish</i>		
Pacific herring	<i>Clupea pallasii</i>	Japan
Black sea bream	<i>Acanthopagrus schlegelii</i>	Japan
Red sea bream	<i>Pagrus major</i>	Japan
Sandfish	<i>Arctoscopus japonicus</i>	Japan
Jacopever	<i>Sebastes schlegelii</i>	Japan
Japanese flounder	<i>Paralichthys olivaceus</i>	Japan
Mud dab	<i>Limanda yokohamae</i>	Japan
Ocellate puffer	<i>Takifugu rubripes</i>	Japan
Striped jack	<i>Pseudocaranx dentex</i>	Japan
Yellow tail	<i>Seriola quinqueradiata</i>	Japan
Sea bass	<i>Lateolabrax japonicus</i>	Japan
Red drum	<i>Sciaenops ocellatus</i>	USA
Spotted sea trout	<i>Cynoscion nebulosus</i>	USA
Striped bass	<i>Morone saxatilis</i>	USA
Mullet	<i>Mugil cephalus</i>	Hawaii
Threadfin	<i>Polydactylus sexfilis</i>	Hawaii
Turbot	<i>Scophthalmus maximus</i>	Denmark, Spain
White sea bass	<i>Atractoscion nobilis</i>	USA
Whitefish	<i>Coregonus lavaretus</i>	Baltic
Cod	<i>Gadus morhua</i> L.	Norway, Sweden, Denmark, Faeroe Islands, USA
<i>Invertebrates</i>		
Kuruma shrimps	<i>Penaeus japonicus</i>	Japan
Chinese shrimps	<i>Penaeus chinensis</i>	Japan
Speckled shrimp	<i>Metapenaeus monoceros</i>	Japan
Mangrove crab	<i>Scylla serrata</i>	Japan
Swimming crab	<i>Portunus trituberculatus</i>	Japan
Blue crab	<i>Portunus pelagicus</i>	Japan
Japanese abalone	<i>Sulculus diversicolor</i>	Japan
Disk abalone	<i>Haliotis discus</i>	Japan
Yezo abalone	<i>Haliotis discus hannai</i>	Japan
Giant abalone	<i>Haliotis gigantea</i>	Japan
Spiny top shell	<i>Batillus cornutus</i>	Japan
Ark shell	<i>Scapharca broughtonii</i>	Japan
Scallop	<i>Patinopecten yessoensis</i>	Japan
Scallop	<i>Pecten maximus</i>	France, Ireland, Norway, UK
Hard clam	<i>Meretrix lusoria</i>	Japan
Hard clam	<i>Meretrix lamarckii</i>	Japan
Giant clam	<i>Tridacna maxima</i>	Indo-Pacific
Giant clam	<i>Tridacna derasa</i>	Indo-Pacific
Surf clam	<i>Spisula sachalinensis</i>	Japan
European lobster	<i>Homarus gammarus</i>	Norway, France, Ireland
Sea urchin	<i>Tripneustes gratilla</i>	Japan
Red sea urchin	<i>Pseudocentrotus depressus</i>	Japan
Sea urchin	<i>Strongylocentrotus intermedius</i>	Japan
Sea urchin	<i>Strongylocentrotus nudus</i>	Japan
Sea cucumber	<i>Stichopus japonicus</i>	Japan

shelf separated from the mainland. Because the larvae were too small to be tagged, no recapture could be registered. The first attempts at scallop enhancement occurred in 1900, but the activity

ceased after a short time. From 1970, stock enhancement started on scallops on a commercial scale in Europe and Japan and from 1980 on giant clams in Indo-Pacific countries. Other invertebrate

enhancement programs started on a commercial basis in 1963 when the government of Japan instituted such actions as a national policy to augment both marine fish populations and commercially interesting invertebrate populations (e.g. abalone, clams, sea urchins, shrimps and prawns).

## Salmonids

Ocean ranching programs of salmon have the longest history and have been most comprehensive. Large programs occur in Japan, along the west coast of North America, and also in the Northern Atlantic. Seven species of salmon, which are all anadromous, have been used for releases of captive-bred individuals: Atlantic salmon (*Salmo salar*) which inhabit the northern Atlantic area and the northern Pacific species: pink (*Oncorhynchus gorbuscha*); Chinook (*O. tshawytscha*); chum (*O. keta*); coho (*O. kisutch*); sockeye (*O. nerka*); and the masu salmon (*O. masou*). Atlantic salmon juveniles remain in fresh water for 1–5 years before they smolt and migrate to the marine environment, whereas the pink and chum leave the rivers soon after they have resorbed the yolk-sac.

The ocean ranching program for chum salmon (*Oncorhynchus keta*) in Japan is typical of the way salmon programs are conducted and is the only program that is considered as economically successful to the operators. Chum fry are easy to produce, their survival is good and the program produces 40–50 million fish annually for the fishermen. The number of chum salmon released during the 15-year period 1980–1995 was stable and was about 2 billion per year, whereas the catches tripled during the same period. More than 90% of the chum salmon catches originated from released juveniles, suggesting an increase in the recapture rate from 1% to 3%. The success of ocean ranching of salmon in Japan was due to favorable environmental conditions over the Northern Pacific, but also due to improvements in marine ranching techniques such as egg collection, artificial diets and timing of release, improvements that also were supported by dietary, physiological and behavioral research.

Salmonids show a wide range of lifestyles and a high phenotypic plasticity. The degree of variation depends on the species. The pink salmon has few life history variants and spawns generally in the gravel of estuaries or the lower parts of North Pacific rivers and then dies. After emergence from the gravel the fry leave immediately for the ocean where they grow to maturity, then return to spawn in their natal gravel at 2 years old. The most complex lifestyles are those of steelhead trout

(*Oncorhynchus mykiss*) ranging from anadromous to landlocked. The species spawn well upriver in the gravel of a stream. On emergence from the gravel, their fry may spend 1–6 years in the river before emigrating to the sea, or they may not emigrate at all, but mature in the juvenile freshwater habitat and reproduce there (in this case they are referred to as rainbow trout). The steelhead is generally iteroparous. The individuals that emigrate to the sea spend 1–6 years there feeding on prey organisms that are not harvested such as krill, copepods, amphipods, mesopelagic fish, but also on commercial species such as capelin, herring and squid before maturing and returning to breed. After spawning they may return to the sea again, mature, and return the next or later years. Through a combination of all these different developmental possibilities, a single cohort of steelhead may give rise to over 30 different life history types.

The length of the spawning period in anadromous salmonids varies and may exceed 3 months in wild populations. The individuals that return early in the spawning season generally produce offspring that hatch early, and grow faster than the fry of those that arrive later. The timing of the returns reflects individual differences in physiological and behavioral strategies for energy storage and usage, and differences in genetic control between individuals with different seasonal runs. The variation in seasonal runs in a population will have implications for survival probabilities of new recruits in fluctuating natural environments and thus for the stability of population sizes over generations. Populations that have long spawning periods exhibit a high degree of phenotypic variation whereas those that have a short spawning period have lower. The more variation there is, the more flexible will the population be in its adaptations to environmental fluctuations. The smaller the variation, the higher the possibility will be for a recruitment failure and for extinction if individuals are semelparous.

When entering the marine environment wild salmonids migrate to highly productive high sea areas where they grow fast. At the onset of sexual maturation most individuals return to the stream where they were spawned after migrating for several years and thousands of kilometers. Exceptions are jacks (males maturing at age 1 year) that remain at sea for a few months; some species remain in coastal waters rather than undergoing long oceanic migrations. Atlantic salmon can return after one sea winter (grilse), two sea-winters and to a lesser extent after three sea-winters. It has been shown that salmon have the ability to recognize distinctive odors of their home stream and that they become

imprinted to this odor as they transform into smolts, just prior to their outward migration. Furthermore, there is evidence that salmon may respond to chemicals (pheromones) given off by conspecifics, such as juveniles inhabiting a stream, and that they are able to discriminate between water that contains fish from their own populations and those from other populations. These abilities allow a great deal of precision in homing. Most commercial harvesting occurs on the coast and recreational and native fishery in the rivers and streams.

Under the salmon enhancement programs it is assumed that the captive-bred released individuals have the same biological and genetic characteristics as wild individuals and that they undertake the same migration routes as their wild conspecifics, and return to their native rivers to spawn. However, it has not been possible to study whether released salmon migrate to the same high seas areas as wild individuals because the main fishery is on the coast and not offshore. The return rates of tagged wild and captive-bred individuals to the various rivers and streams have been compared and show that the homing instinct is not always 100% in any of the groups; the straying rate is three times as high for captive-bred fish with up to 13% recaptured in a different location than where the individuals were released. This suggests different homing instinct abilities in captive-bred and wild salmonids.

The nature of genetic variation within species that are part of ocean ranching programs was not appreciated when they started. The goal of ocean ranching was to restore wild stocks to their former abundance and so to restore the fishery to its former levels. No attention was paid to the number of spawners that were required in order to obtain sufficient genetic variation among captive-bred fish. Often the effective number of spawners was low, resulting in reduced genetic diversity of the population. Moreover, individuals from the broodstock were often taken from the first adults to return, and fry from early-spawning adults were hatched in captivity and released on the spawning grounds together with offspring from fish that had spawned in the wild. Such actions may have had a negative influence on the genetic diversity of the mixed population of wild and captive-bred fish because the fry that hatched early, grow faster, and can displace fry of later-spawning fish. For example, in the USA a decrease in the spawning season from 13 to 3 weeks over just 13 years has been demonstrated for coho salmon. It has also been reported that offspring of captive-bred steelhead that spawned naturally had much lower survival than those from wild fish. This could be a contributing

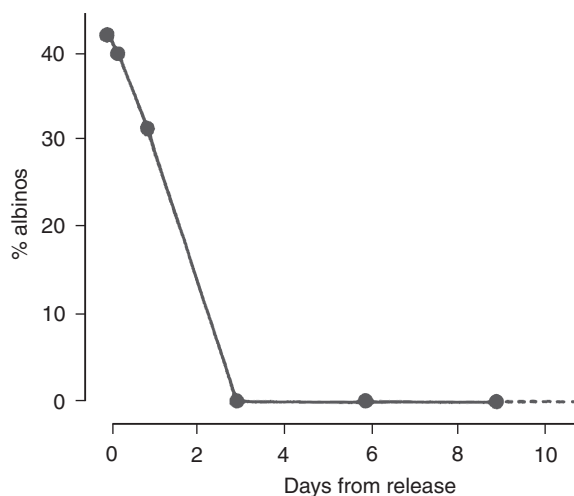
factor to the continuing decline in enhanced salmon stocks despite large-scale releases.

## Marine Fish

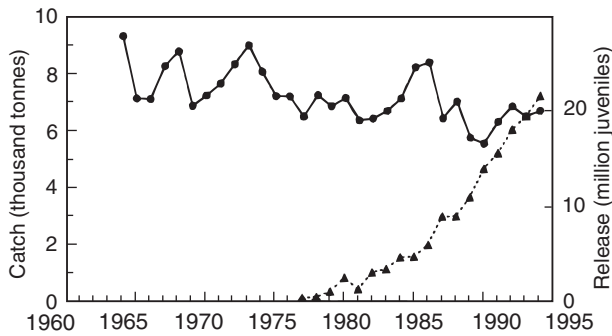
Ocean ranching is practiced on many marine fish in several countries; the Japanese programs are the largest. Captive-bred individuals of eleven marine fish species are released on a commercial basis in Japan (Table 1) with a total yearly release of 68 million fry or juveniles. Red sea bream (*Pagrus major*) and Japanese flounder (*Paralichthys olivaceus*) are released in highest quantities (22 million of each per year).

Juvenile Japanese flounder are 4–12 cm long when released. Those that are larger than 9 cm at release survive to commercial size. Captive-bred individuals show a high degree of partial or complete albinism on the ocular side and characteristic melanin deposits on the other side. These juveniles suffer from high mortality immediately after release (Figure 1). The proportion of the catches that have a captive origin is used to quantify impact on catches. Between 10 and 40% of the catches consist of released fish; but this program cannot be considered as a success. Despite releases having increased from 5 million to 22 million juveniles from 1985 to 1995, the total catch of flounder is decreasing (Figure 2).

There is also a size-dependent survival of red sea bream; up to 50% are reported in catches if fish were 4 cm at release. Enhancement of red sea bream has been conducted since 1974 and mostly 4-cm-long individuals are now released. However, the population continues to decline despite the releases (Figure 3).



**Figure 1** Change in the proportion of albino Japanese flounder juveniles in the catch for successive days after release. (After Blaxter, 2000.)

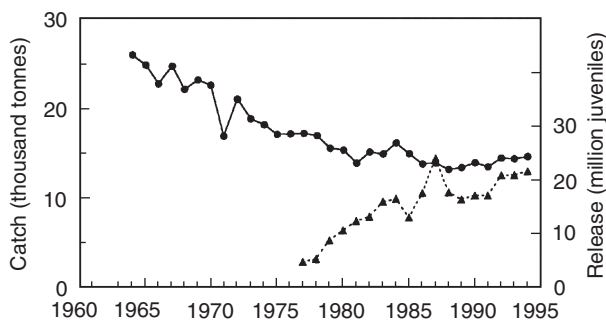


**Figure 2** The catch (●) and number of released juveniles (▲) of flounder in Japan. (After Masuda and Tsukamoto, 1998; in Coleman *et al.*, 1998.)

Ten other marine fish species (Table 1) are used for ocean ranching, but most can be considered to be at an experimental stage. Only the red drum (*Sciaenops ocellatus*) and spotted sea trout (*Cynoscion nebulosus*), which are being released in Texas lagoons of the Gulf of Mexico, have reached a commercial scale. Since the early 1980s there have been yearly releases of 16–30 millions of red drum fingerlings and 5 million sea trout. The adult populations of red drum live offshore and the eggs and larvae are swept into the inshore areas and lagoon where they grow to juveniles for up to six years, and where they support a recreational, and sometimes a commercial fishery. The proportion of released individuals in the catches has been as high as 20%.

### The First Scientific Evaluation of Stock Enhancement; The Norwegian Cod Study

The most comprehensive scientific study on marine fish stock enhancement has been conducted on Atlantic cod. Average age at maturity in coastal cod is 3 years. Spawning occurs at grounds located at *c.* 50m depth and the spawning period is February–April. In western Norway juveniles settle in the



**Figure 3** The catch (●) and number of released juveniles (▲) of red sea bream in Japan. (After Masuda and Tsukamoto, 1998; in Coleman *et al.*, 1998.)

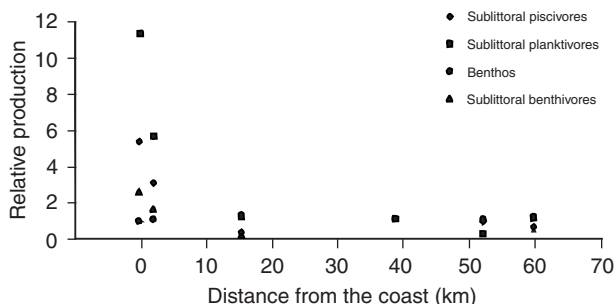
shallow near-shore areas during summer and early fall and inhabit mainly 0–20m depth. There is a commercial and recreational fishery for cod. Cod enter the fishery as by-catch when 6 months old, but most are harvested when two years or older. Coastal cod remain localized in the fiords at least until maturation. Tagging experiments have shown that very few individuals migrate to other areas. Because of this resident life history, cod need to feed on local prey or on prey that are advected into the fiords. This is very different from salmonids that move to high sea areas and bring biomass ‘home’ to the fishery.

Despite the failure of releases of yolk-sac larvae, new attempts with ocean ranching of cod commenced in Norway in 1983 first through large-scale experiments, but later as small-scale experiments also in Sweden, Denmark, the Faroe Islands and USA. The new approach was to release 6–9-month-old juveniles, 10–20cm long. This was decided because a positive correlation had been documented between abundance at 6–9 months old and subsequent recruitment to the fishable population, and because large-scale production techniques for juvenile cod had been developed by the Institute of Marine Research in Norway.

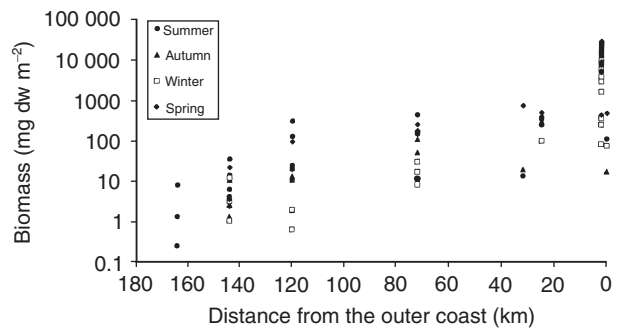
The very extensive work on cod by the Norwegians is thought to represent the most thorough investigation of the possibilities and limitations of stock enhancement. A large governmental interdisciplinary research program was initiated in 1983 with experiments being carried out in a number of fiords along the coast. The aim was to develop full-scale production of juveniles, to develop techniques for mass marking and to design and carry out large-scale release experiments on the Norwegian coast. These were to be in association with wide-ranging field studies which were intended to evaluate the potential and limitations of sea ranching of cod from an ecological perspective, before ocean ranching was initiated on a commercial scale. Masfjorden was selected for the study of the whole ecosystem and its dynamic fluctuation in carrying capacity. Research here involved field studies before and after large-scale releases. In addition dynamic ecosystem simulation models were developed. The models integrated all relevant field data and were used to study the effect on fish production and carrying capacity of environmental and biological factors. It was shown that although juvenile wild cod populations were augmented after release of captive-bred cod, there was no sign of stock enhancement of 2-year-old cod when these should have recruited to the fishery. A recent time-series analysis of the survival of captive-bred cod from this

fiord shows a high mortality rate in the spring at one year old. It is uncertain what causes this. One possibility is a higher mortality risk in captive-bred than wild cod in spring when there is a massive immigration of spurdog and also higher abundance of other predators. The modeling predicted that density-dependent growth, predation, and cannibalism restricted cod productivity, and that the most important environmental factor was nonlocal wind-driven fiord-coast advection of organisms at lower trophic levels. This limited the carrying capacity for fish at higher trophic levels in the fiord. The zooplankton *Calanus finmarchicus*, which in spring and summer occur in high abundance in the coastal waters of Norway, were exchanged between coast and fiord via advection of intermediate water-masses. These are the main prey of gobies, and gobies are the main prey of juvenile cod. If strong southerly winds occur frequently, they transport planktonic organisms into the fiord, whereas if strong northerly winds occur most frequently, they may reduce the abundance of planktonic organisms within the fiord and thus limit the carrying capacity for fish at higher trophic levels. This means that the carrying capacity of resident fish in local habitats is highly dependent on environmental processes that occur on a larger scale. The modeling also predicted that the distance from the coast affected the carrying capacity and individual growth of fish in the fiords with lower production and growth within the inner fiords than on the coast (Figure 4) because the advection rate and zooplankton density become damped with increasing distance from the coast (Figure 5). This was confirmed by empirical estimates of growth curves for cod (Figure 6).

As a consequence of the negative conclusion of the Norwegian experimental ocean ranching on cod, the releases were terminated and it was decided not to scale up to commercial level. The research has, how-

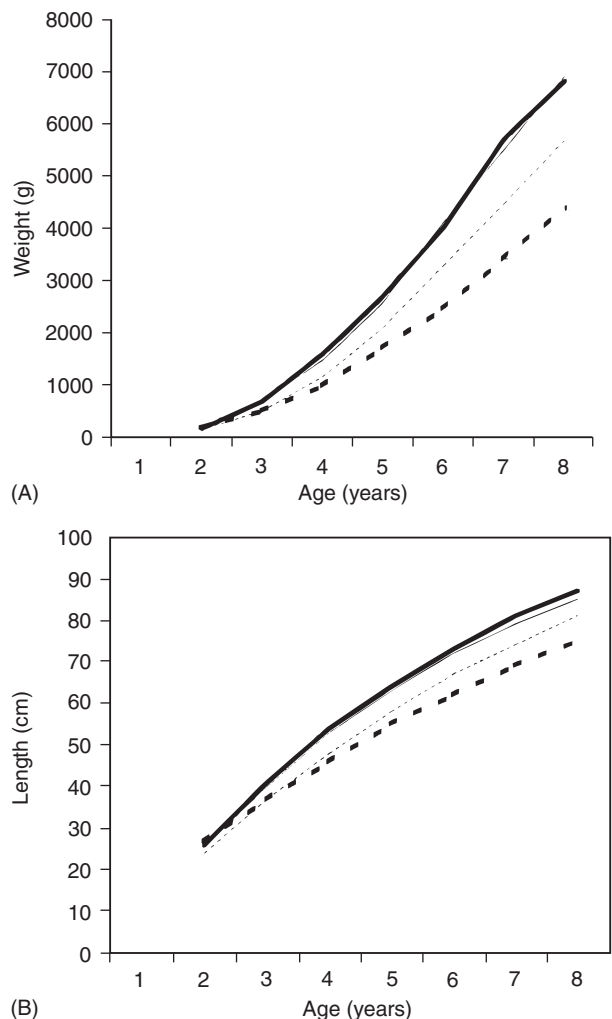


**Figure 4** Simulated yearly production for five west Norwegian fiords located at different distances from the outer coast. Sublittoral planktivores refers to gobies, sublittoral piscivores refers to cod and other fish at the same trophic level. (After Salvanes *et al.*, 1995.)



**Figure 5** The density of *Calanus finmarchicus* as a function of the distance from the coast by season. Note the logarithmic scale on the biomass axis. (After Salvanes *et al.*, 1995.)

ever, not been wasted. New insights into fiord ecology and particularly the influence of environmental factors on ecosystem dynamics have been achieved.



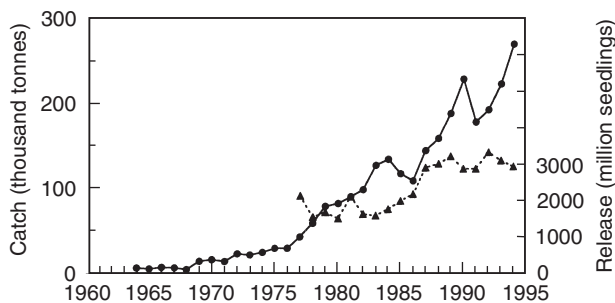
**Figure 6** Growth curves ((A) weight; (B) length) for released and wild cod. —, wild cod, outer coast; - - -, wild cod, inner fiord; —•—, released cod, outer coast; - -•- -, released cod, inner fiord. (Modified from Svåsand *et al.*, 2000.)

## Marine Invertebrates

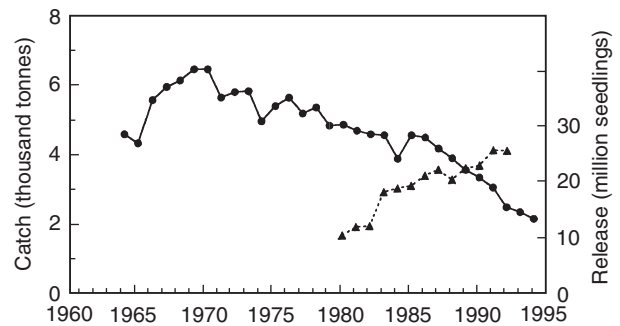
Enhancement programs on invertebrates are most comprehensive in Japan, including shrimps, crabs, abalone, clams, scallops, sea urchins and sea cucumber (Table 1). The present program started on a commercial basis around 1970. Annual releases of seedlings are  $3.47 \times 10^9$ , mostly of scallop (*Patinopecten yessoensis*) ( $3 \times 10^9$ ).

Scallop seabed culture of *Pecten maximus* started in Europe in France in 1980 and extended to Ireland, Scotland, and Norway. Each country produces 25 million juveniles per year for release. Juveniles are first kept in intermediate culture for 1–2 years before release. In France 3 cm juveniles are released on seabeds, whereas in Norway they are 5–6 cm before being released. Ocean ranching with scallops in Japan is considered successful because the landings have increased from 5000 tonnes around 1970 to 200 000 tonnes in the mid 1990s (Figure 7). Other invertebrate populations in Japan are, however, still declining despite the high numbers of released seedlings. For example, the populations of abalone have more than halved over the last 25 years (Figure 8).

The benefits of releasing invertebrates is that they are either stationary or do not move far from the release point and that they feed lower in the food web than the fish and therefore utilize a larger proportion of the primary production. For example bivalves benefit from transferring locally produced algae to highly valuable biomass by filter feeding; others such as prawns, shrimps and crabs feed on locally produced or advected secondary producers. However, the drawback is that often juveniles that are being released are small and grow much more slowly than fish of the same age and suffer from high predation mortality. Moreover, some species do not move very much, and if juveniles are released in high densities, this could result in unwanted den-



**Figure 7** The catch (●) and the number of released seedling (▲) of scallop in Japan. (After Masuda and Tsukamoto, 1998; in Coleman *et al.*, 1998.)



**Figure 8** The catch (●) and the number of released seedlings (▲) of abalone in Japan. (After Masuda and Tsukamoto, 1998; in Coleman *et al.*, 1998.)

sity-dependent mortality (predation, food competition). In addition, the production costs of viable seedlings are often high.

One example of a slow grower is the European lobster. In the 1970s, Norway succeeded in producing one-year-old juveniles for release, and soon thereafter a commercial lobster hatchery with a production capacity of 120 000 juveniles per year was built. These have been released along the Norwegian coast in attempts to rebuild depleted populations. A large-scale experiment has been conducted at Kvitsøy, a small island with its own continental shelf, located on the south-western coast of Norway. It took 5–8 years after the first large releases in 1985 and 1986 before the lobster recruited to the regulated commercial fishery. Although captive-bred individuals were not tagged, it was possible to distinguish them from the wild because most had developed two scissors claws instead of the normal one scissors and one crusher claw. From 1990 to 1994 the released juveniles were microtagged. In 1997 43% of the landings were of released lobster. The landings of lobster increased from 1995 to 1997, but catches of the wild stock showed a weak decrease. It is not known whether released lobsters replace wild stock.

## Measuring the Success of Ocean Ranching

All enhancement programs rely on the assumptions that human operations have reduced populations to sizes below the carrying capacities, or that there are possibilities for increased production of the target species, and that releases of captive-bred juveniles will increase the number of adults and thus subsequent harvests. However, few attempts have been made to test these assumptions scientifically due to their complexity, and many questions are therefore still unanswered.

Ocean ranching programs involve enormous investments, but the pay-off has been difficult to evaluate and therefore generally ignored. The evaluation should be done in two steps; first biologically and then economically. The measure of the success of an enhancement program depends on the objectives: the fishermen consider it successful if they catch more fish; biologists at the hatcheries may consider the production and release of viable juveniles as a success; a conservation biologist will be happy if previously nearly extinct populations increase again; an ecologist will also demand that increased biological production on the target species does not have negative influence on wild conspecifics or on other parts of the ecosystem; and an economist will only consider it a success if there is a positive net pay-off of investments.

The first stage of an evaluation is to determine if there is a net biological benefit by: (1) estimating survival of released fish; (2) verifying survival over many generations; (3) measuring eventual negative effects on wild fish or on the ecosystem as a whole by covering questions such as: does individual variation in growth and abundance change? The final stage would then be to evaluate eventual economic benefit. The programs that occur today usually have immediacy and an applied aspect, and investments into experimental ecology to test major underlying assumptions for increased biological production have therefore been ignored. From a biological point of view this is very shortsighted as the absence of proper evaluation means that ocean ranching programs are conducted in an *ad hoc* way and this will result in a high chance of investment for nothing.

Fish populations have fluctuated in the periods before fishing technology allowed high fishing pressure. It has been reported that some of the marked shifts in sockeye salmon abundance over the last 300 years were associated with climatic changes long before humans were able to overfish. The way climate affects cycles in population sizes is, however, difficult to separate from human made effects. If fish are released because a population declines, and if such releases are conducted during a time period when there are unfavorable climatic conditions, the negative climatic factors may counteract positive enhancement effects. For example, the simulation modeling of the Masfjorden ecosystem showed that nonlocal wind-driven coast-fjord advection of organisms at lower trophic levels had a large impact on the carrying capacity of the cod populations. This means that carrying capacities for fish in coastal ecosystems fluctuate in an unpredict-

able manner. Simulations also suggest that with imperfect knowledge of the carrying capacity for juvenile cod – which represents more or less the current situation – it is impossible to conduct ‘perfect releases’ that match the carrying capacity. This means that there may be no payoff from releasing cod to increase a stock.

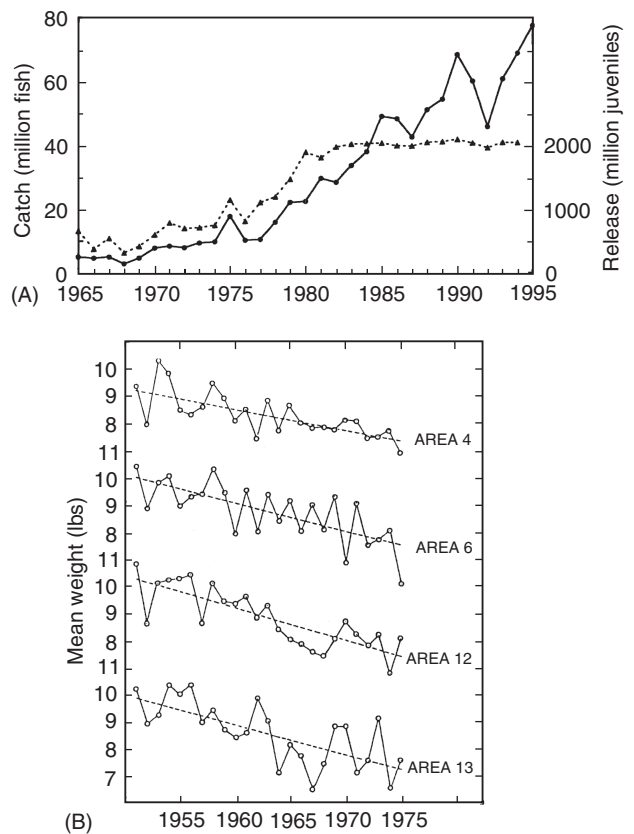
Other major questions concern the ecology of wild stocks, and also whether the captive-bred individual's genetic, physiological, morphological and behavioral traits are similar to those of wild conspecifics. If not, are these factors deviating so much that released individuals have poorer or better survival than wild conspecifics? Hence, will enhancement effects disappear soon after release or will released animals just replace wild and therefore not enhance total population sizes (released and wild) and harvests? For example in salmon groups size hierarchies among juveniles soon develop in their nursery streams; this also happens among adults in the spawning habitats. Large juveniles tend to monopolize the best feeding spots, and on the spawning beds the large adults get access to the best gravel beds and large males have higher mating success with females. Mature escaped farmed salmon enter Norwegian rivers. Here they often replace wild fish on the spawning grounds. This can be a long-term problem due both to the way the farmed salmon has been domesticated and selectively bred for rapid growth and late maturation, and to a life history that would not necessarily have any benefit under all environmental situations if they escape to the wild. Moreover, offspring of captive-bred steelhead that spawned naturally had much lower survival than those from the wild. It is possible that instead of enhancing a population, large-scale releases of captive-bred individuals can first replace wild conspecifics, and thereafter become extinct over a few generations in extreme environmental conditions to which the released fish are not adapted. Hence, differences in the life history of captive-bred and wild fish can be a contributing factor to the continuing decline in enhanced salmon stocks despite large-scale releases. If enhancement programs are initiated without taking into consideration the genetic diversity the wild populations have evolved through generations and that is required for survival under extreme environmental fluctuations, the program may fail.

Another documented difference between captive-bred and wild fish is the capability of the latter to show flexible behavior under changing environmental conditions. Captive-bred cod and salmonids adapt more slowly than wild fish to novel food or to food encountered in a different way than previously.



They also tend to take more risks than do wild fish. When captive-bred cod were released for sea ranching in Masfjorden off western Norway, it was evident from field samples that these fish had a different diet and higher mortality rate than wild cod at least for the first three days after release. Moreover, these captive-bred cod were released into the natural habitat in numbers that greatly exceeded that of wild cod of the same cohort. Despite this, released cod abundance declined sharply during the spring when the fish were one-year-old, six months after release. At release these fish were naive to the heterogeneous marine environment, to predators, and also to encounters with natural prey. It is possible that feeding behavior, and perhaps also other behavior, of captive-bred animals differed from that of wild cod over a much longer time than the first three days after release and that this could have made them more vulnerable toward piscivorous predators. Released salmonids also do less well than wild. Although they were able to adapt to novel and/or live prey by learning for some days or weeks before they were released, they took less prey, grew more slowly, had a higher mortality rate than wild, had a narrower range of dietary items and frequently lagged behind wild fish in switching to new prey items as these became abundant.

In the literature there is hardly any ocean ranching program that can be considered successful on both ecological and economic grounds. Only the chum salmon ranching program in Japan is considered economically successful, at least for the operators, because the cost of fry production is low and the fishery catches more fish (Figure 9A). There are, however, two possible drawbacks even for this program: the average size of individual chum has been decreasing (Figure 9B), and the change is correlated with the Japanese chum releases, and with the abundance of chum in the North Pacific. The economic value of individual fish has therefore decreased. Moreover, total Pacific chum production has only increased by 50% since 1970, and the North American production (largely natural) increased by about the same amount. It might thus be that the apparent increase in Japanese chum production could be due to favorable climatic conditions in combination with replacement of wild fish. It is, however, very difficult to separate enhancement and environmental effects. Nevertheless, cyclical changes in Pacific salmon populations have occurred earlier and long before humans were able to overfish or conduct captive breeding for release. This means that environmental factors would mask any cause of change in populations that are seen in populations



**Figure 9** (A) The catch (●) and the number released of juveniles (▲) of chum salmon in Japan. (B) Changes in the mean weights of coho salmon harvested from the Pacific ocean between 1950 and 1981. (After Masuda and Tsukamoto, 1998; in Coleman *et al.*, 1998.)

chosen for ocean ranching. Another study, on chinook salmon of the Columbian river basin showed that the population continues to decline towards extinction despite the release of captive-bred individuals. It was concluded through simulation studies that the only way to reverse the decline would be to increase the survival of first-year fish, and the only way of doing this might be to remove the dams that had been constructed for hydropower production.

The prospects of marine ranching should be critically evaluated biologically and economically before commercial large-scale programs are initiated on a target species. The optimal species for stock enhancement should be easy and cheap to rear to release size, it should grow fast, have a low mortality rate and it should feed low in the food chain. It should also have a behavior that does not deviate from wild conspecifics or lead to negative effects on other species. However, the case studies reported here illustrate clear difficulties in increasing population sizes by releasing captive-bred individuals and

show that hardly any commercial enhancement program can be regarded as clearly successful. Model simulations suggest, however, that stock-enhancement may be possible if releases can be made that match closely the current ecological and environmental conditions. However, this requires improvements of assessment methods of these factors beyond present knowledge. Marine systems tend to have strong nonlinear dynamics, and unless one is able to predict these dynamics over a relevant time horizon, release efforts are not likely to increase the abundance of the target population.

## See also

**Mariculture, Environmental, Economic and Social Impacts of. Salmonid Farming. Salmon Fisheries: Atlantic; Pacific. Salmonids.**

## Further Reading

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# OCEAN SUBDUCTION

**R. G. Williams**, University of Liverpool, Liverpool, UK

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## Introduction

Ocean subduction involves the transfer of fluid from the mixed layer into the stratified thermocline (Figure 1). The upper ocean is ventilated principally through the subduction process, while the deep ocean is ventilated through open-ocean convection and cascading down coastal boundaries. The term ‘ocean subduction’ makes the geological analogy of a subduction zone where a rigid plate of the Earth’s

lithosphere slides beneath a more buoyant plate and into the hotter part of the mantle.

Ventilation connects the atmosphere and ocean interior through the transfer of fluid from the surface mixed layer into the ocean interior. Water masses are formed in the surface mixed layer and acquire their characteristics through the exchange of heat, moisture, and dissolved gases with the atmosphere. When the water masses are transferred beneath the mixed layer, they are shielded from the atmosphere and only subsequently modify their properties by mixing in the ocean interior. Hence, the ventilation process helps to determine the relatively long memory of the ocean interior, compared with the surface mixed layer.